monas producing a brown rot (not to be confused with *P. campestris*, E. F. Smith), which I am at present studying, works in a totally different manner; its action is very much slower, and the rapid swelling of the cell-wall, as described above, is not a conspicuous feature.

"The Influence of Varying Amounts of Carbon Dioxide in the Air on the Photosynthetic Process of Leaves and on the Mode of Growth of Plants." By HORACE T. BROWN, LL.D., F.R.S., and F. ESCOMBE, B.Sc., F.L.S. Received April 28,—Read May 29, 1902.

[PLATES 5—10.]

In a paper recently laid before this Society dealing with the physical processes which regulate the entry of atmospheric carbon dioxide into the leaves of plants,* we incidentally described a series of experiments relating to the rate of absorption of dilute gaseous carbon dioxide by surfaces of solutions of caustic alkali, when air containing definite small amounts of this gas is drawn over the liquid. Contrary to what might be expected from the perfect absorbing nature of the solution, and the known laws of gaseous diffusion, the amount of CO_2 absorbed by unit area of the liquid surface in unit time ceases sensibly to increase when a comparatively low velocity of the moving air current has been reached. This, however, only holds good when the proportion of CO_2 in the air stream is maintained quite constant, any slight variation in the amount at once affecting the rate of absorption. On investigation it was found that for dilutions of carbon dioxide lying between 0·6 part and 6 parts per 10,000 of air, the rate of absorption of the carbon dioxide *is strictly proportional to its partial pressure.*†

In determining the rates of gaseous diffusion of atmospheric carbon dioxide through multiperforate diaphragms extended over chambers containing perfect absorbents, the same relations between partial pressure of the gas and its absorption were found to hold good: under these conditions the amount of carbon dioxide passing through the

* 'Phil. Trans.,' B, 1900, vol. 193, p. 278.

† So accurately is this the case that the process, which is described in detail in the above-mentioned communication, may be used for determining the varying amounts of CO_2 in air without the necessity of measuring the volume of air which passes through the apparatus. It is merely necessary to pass the air over the absorbing surface at a sufficient rate to ensure maximum absorption, and to compare this amount of absorption in a given time with that produced from air of a known content of carbon dioxide, a process of standardisation which is done once for all with the apparatus. The ratios of the absorptions give at once the ratios of the partial pressures of the CO_2 in the two cases.

2 E 2

diaphragm in a given time is also directly proportional to the density of that gas in the moving stream of air which flows over the outer surface of the diaphragm.

But this latter case exactly defines the physical conditions under which atmospheric carbon dioxide enters the tissue of a living leaf, the multiperforate diaphragm being represented by the cuticle and epidermis, pierced with numerous stomata, and the inner absorbing chamber by the intercellular spaces of the parenchyma, bounded by the chlorophyll-containing cells in which the process of photosynthesis goes on (*loc. cit.*).

From these considerations one would be led to expect that under conditions favourable for photosynthesis, such as are fulfilled by the incidence of a sufficient amount of the right kind of radiant energy, a living leaf would be able to absorb amounts of carbon dioxide from the surrounding air which, within certain limits of concentration, are directly proportional to the partial pressures of that gas.

One essential condition would of course be that the actively assimilating organs of the leaf in which the photosynthesis takes place should act as *perfect* absorbers, that is to say, they must be able to deal with the carbon dioxide as fast as it is brought within their sphere of influence by the physical processes of diffusion. When this condition is no longer fulfilled, either through lack of a sufficient amount of radiant energy of the right wave-length reaching the active centres of photosynthesis, or through the natural limit of the metabolic activity of those living units having been reached in other directions, we should then expect the intake of the gas into the leaf to be no longer proportional to its partial pressure in the outer air.

We have been able to verify these deductions experimentally, and to show that a living leaf is really able, within certain limits, to respond to increased amounts of carbon dioxide in the air surrounding it, in such a manner as to indicate an approximate proportionality between the photosynthetic work it can accomplish, and the partial pressure the gas exercises in the air bathing the leaf surface.

In these experiments the leaves, which were in some instances still attached to the plant, had their laminæ enclosed in air-tight glazed cases, through which was aspirated a sufficiently rapid stream of air the volume of which was determined by means of carefully standardised meters. The carbon-dioxide content of the air was determined both before and after its passage over the leaf, and the area of the leaf was also accurately known. A full description of the apparatus employed will be given in a subsequent paper; it was so arranged that large volumes of air could be employed, containing known amounts of carbon dioxide either larger or smaller than the normal amount in the atmosphere.

Experiment I.—In this case comparative experiments were made on

two successive days in August, 1898, with two similar leaves, A and B of *Helianthus annuus*, whilst still attached to the plant. These were exposed to the strong diffused light of a clear northern sky under as nearly as possible identical conditions, with the exception of the composition of the air drawn through the cases.

Over leaf A was drawn normal air containing 2·8 parts per 10,000 of CO_2, whilst the air passing over leaf B contained 25·53 parts CO_2 per 10,000.

Leaf A.

Area of leaf	743 ·1 sq. cm.
Volume of air passed per hour, reduced to normal temperature and pressure	159 ·03 litres.
CO_2 content of air entering case	2 ·80 parts per 10,000
,, ,, leaving case	1 ·64 ,, ,,
Mean CO_2 content of air in contact with leaf during experiment	2 ·22 ,, ,,
CO_2 absorbed by leaf per hour	18 ·44 c.c.
,, per sq. metre per hour	248 ·2 c.c.

Leaf B.

Area of leaf	863 ·75 sq. cm.
Volume of air passed per hour reduced to normal temperature and pressure	72 ·7 litres.
CO_2 content of air entering case	25 ·30 parts per 10,000
,, ,, leaving ,,	4 ·12 ,, ,,
Mean CO_2 content of air in contact with leaf during experiment	14 ·82 ,, ,,
CO_2 absorbed by leaf per hour	155 ·7 c.c.
,, per sq. metre per hour	1802 ·8 c.c.

It is manifest that if we wish to determine the relation of the partial pressures of carbon dioxide to the rate of intake of that gas into the leaf, we must employ the values representing the mean carbon-dioxide content of the air in contact with the leaf during the experiment, which may be taken as the arithmetical mean of the composition of the entering and emergent air. In the above experiment we obtain the following relations:—

Ratio of partial pressures of CO_2 in A and B, 2·22 : 14·82 or **1 : 6·6**.
Ratio of CO_2 absorbed per sq. metre of Leaf A and B in 1 hour, 248·2 : 1802·8 = **1 : 7·2.**

Thus by increasing the amount of CO_2 in the air passing over the leaf about sevenfold, we have, under similar conditions of illumination, increased the photosynthetic power of the leaf by a little more than the same amount.

Experiment II.—In this instance two similar leaves, A and B, of *Helianthus annuus* (cut from the plant, and with their petioles immersed in water) were exposed on August 25, 1899, to sunlight under a

thin white canvas screen, the separate glazed cases containing the leaves being placed side by side under exactly similar conditions. The duration of the experiment was 4 hours.

Through case A ordinary air was passed, and through case B air enriched with CO_2 up to 13·1 parts per 10,000 :—

Leaf A.

Area of leaf	336·4 sq. cm.
Air passed in 4 hours (N.T.P.)	378·82 litres.
" 1 hour	94·70 "
CO_2 content of air entering case	2·80 parts per 10,000
" " leaving "	1·70 " "
Mean CO_2 content of air in contact with leaf during experiment	2·25 " "
CO_2 absorbed by leaf per hour	10·39 c.c.
" " per sq. metre per hour	309 c.c.

Leaf B.

Area of leaf	312·7 sq. cm.
Air passed in 4 hours (N.T.P.)	325·59 litres.
" 1 hour "	81·39 "
CO_2 content of air entering case	13·1 parts per 10,000
" " leaving "	6·8 " "
Mean CO_2 content of air in contact with leaf during experiment	9·95 " "
CO_2 absorbed by leaf per hour	51·25 c.c.
" per sq. metre per hour	1639 c.c.

The ratio of partial pressures of CO_2 in A and B is 2·25 : 9·95 = **1 : 4·4.** The ratio of CO_2 absorbed per sq. metre per hour in A and B is 309 : 1639 = **1 : 5·3,** so that there is again a fair correspondence of the ratios.

Many other similar experiments were made, of which the two quoted are typical examples. In all cases where the illumination of the leaf was good, although the amount of intake of CO_2 into the leaf was approximately proportional to the increased partial pressure, the photosynthetic work of the leaf was always somewhat in excess of what might be expected from the increased amount of CO_2.

This is probably due to the fact that under the particular conditions of the experiment the air which was more highly charged with the gas also contained a little more moisture than the ordinary air. Under these circumstances the stomata of the B series would tend to open a little more than those of the A series, a fact which would in itself account for the correspondence between partial pressures and intake not being so perfect as it would otherwise have been, since, other things being equal, the intake is proportional to the linear dimensions of the openings.

In the two following experiments, where the illumination of the leaves was of *low intensity*, the differences are in the other direction,

the increased amounts of CO_2 in the air passed over the leaf being evidently in excess of the power of the assimilatory centres to deal with them. In such cases the ratios of intake are necessarily considerably lower than the ratios of the partial pressures.

Experiment III. Under Insufficient Illumination.—In this instance the day (August 29, 1899) was very cloudy, with rain falling during nearly the whole time.

Cut leaves of *Helianthus annuus* A and B were placed in adjoining cases as in the other experiments.

Leaf A.

Area of leaf	275·9 sq. cm.
Air passed in $3\frac{1}{4}$ hours (N.T.P.)	287·94 litres
„ 1 hour	88·5 „
CO_2 content of air entering case	2·80 parts per 10,000
„ „ leaving „	1·70 „ „
Mean CO_2 content of air in contact with leaf during experiment	2·25 „ „
CO_2 absorbed by leaf per hour	9·7 c.c.
„ per sq. metre per hour	351 c.c.

Leaf B.

Area of leaf	411·2 sq. cm.
Air passed in $3\frac{1}{4}$ hours	248·17 litres.
„ 1 hour	76·3 „
CO_2 content of air entering case	21·3 per 10,000
„ „ leaving „	11·5 „
Mean CO_2 content of air in contact with leaf during experiment	16·4 „
CO_2 absorbed by leaf per hour	74·8 c.c.
„ per sq. metre per hour	1819 c.c.

Ratio of partial pressures of CO_2 in A and B, 2·25 : 16·4 = **1 : 7·2.** Ratio of CO_2 absorbed per square metre per hour in A and B, 351 : 1819 = **1 : 5·1.**

Experiment IV.—A similar experiment under *insufficient illumination* on leaves of *Catalpa bignonioides*, August 31, 1899. The sky was very dark, with some rain, and only a few gleams of partial sunlight near the close of the experiment.

Leaf A.

Area of leaf	417·6 sq. cm.
Air passed in 4 hours (N.T.P.)	304·33 litres.
„ 1 hour	76·08 „
CO_2 content of air entering case	2·80 per 10,000
„ „ leaving „	1·30 „
Mean CO_2 content of air in contact with leaf during experiment	2·05 „
CO_2 absorbed by leaf per hour	11·41 c.c.
„ per sq. metre per hour	273·2 c.c.

Leaf B.

Area of leaf	433·6 sq. cm.
Air passed in 4 hours (N.T.P.)	250·1 litres.
,, 1 hour	62·51 ,,
CO_2 content of air entering case	16·1 per 10,000
,, ,, leaving ,,	9·2 ,,
Mean CO_2 content of air in contact with leaf during experiment	12·65 ,,
CO_2 absorbed by leaf per hour	43·12 c.c.
,, per sq. metre per hour	994·4 c.c.

Ratio of partial pressures of CO_2 in A and B, 2·05 : 12·65 = **1 : 6·1.** Ratio of CO_2 absorbed per square metre per hour in A and B, 273·2 : 994·4 = **1 : 3·6.**

These experiments, and many others of a similar nature which might be quoted, indicate beyond a doubt that, at any rate for a short period, the photosynthetic functions of the leaf lamina are capable of being intensified by increasing the amount of carbon dioxide in the surrounding air, and that under favourable conditions the response of the leaf in this direction is approximately directly proportional to the amount of CO_2 present.

Experiments of this nature are necessarily limited to comparatively short periods, and give us no information as to how far the plant, as a whole, will respond to such changes in its atmospheric environment. When first drawing attention to these facts in 1899* it was pointed out by one of us that we were not justified, without direct experiment, in concluding that the plant would be able to avail itself indefinitely of the increased amount of plastic carbohydrate material formed in its leaves under these artificial conditions, and that translocation, metabolism, and growth may have become so intimately correlated that the perfect working of the entire plant may only be possible in an atmosphere containing the normal amount of three parts of CO_2 per 10,000.

In approaching this question experimentally we were led to make certain preliminary experiments with a view to seeing how far slightly increased amounts of carbon dioxide in the air would affect the actual dry weight of plants grown in such an atmosphere. Should there be any influence on the plant throughout its growth in any way comparable in magnitude with that of the increased photosynthesis in leaves it could not possibly escape detection, even when using atmospheres containing only two or three times the normal amount of CO_2.

Experiment V.—Two seedling plants of *Vicia Faba* were chosen which had been grown in pots, and which were of the same age and as nearly similar in appearance as possible. Above each of the pots was placed a circular metal tray with a large central aperture, and an annular rim which formed a water-seal for a large inverted glass beaker. The stem

* Presidential Address, British Association, Section B, Dover.

of each of the young plants was passed through a split cork fitted into the central hole of the tray, and was luted air-tight with a soft mixture of vaseline and paraffin. Two narrow tubes also passed through the tray, one of which was cut short inside whilst the other extended to the top of the glass covering the vessel. A slow current of moist air was aspirated through each inverted beaker. In one case ordinary air was used, containing from 2·8 to 3 parts of CO_2 per 10,000, whilst in the other the air stream was enriched with CO_2 to the extent of 5·4 parts per 10,000 by passing through a small glass tower containing marble, over which a regulated amount of very dilute hydrochloric acid was slowly dropped. In this latter instance the air-stream was passed through a wash-bottle containing a solution of sodium bicarbonate before it entered the chamber containing the plant. In the control experiment with ordinary air only water was used in the wash-bottle.

The extra carbon dioxide was only supplied during the daytime, whilst during the night both chambers were supplied with ordinary air. The experimental chambers were placed side by side in a well-lighted greenhouse under exactly equal conditions of temperature, direct sunlight being prevented from reaching the plants.

The experiment in this instance lasted for 11 days, extending from June 29 to July 10, 1899.

The plants, which were almost identical in appearance, were then carefully washed out of their pots, and with their roots were dried and weighed.

Dry Weight of Plants.

A. Grown in normal air	0·856 gramme.
B. Grown in air containing double the normal amount of CO_2	0·843 „

Experiment VI.—Another similar experiment with *Vicia Faba.*

In this case beans of as nearly an equal weight as possible were germinated in pots, and a selection from the seedlings was made of well-developed plants of similar appearance.

The CO_2 was in one case increased to twelve parts per 10,000, *i.e.*, four times the normal amount, ordinary air being passed over the other plant. The experiment lasted 10 days, from August 19th to August 29th, 1899.

Dry Weight of Plants.

A. Grown in normal air	0·872 gramme.
B. Grown in air containing four times the normal amount of CO_2	0·814 „

The *foliar area* was also measured in this instance, with the following result :—

A.	Area of leaves on plant in normal air	66·9 sq. cm.
B.	,, ,, in air with four times normal amount of CO_2...	55·6 ,,

Similar results were also obtained with young plants of *Helianthus annuus*.

The experiments indicate that the plants were certainly not stimulated to increased growth by somewhat increasing the amount of CO_2 in the surrounding air. The evidence in fact points in the other direction, *i.e.*, towards a slight diminution in the increment of dry weight, and to a less development of foliar area. There were also indications of certain morphological differences, which assumed some importance in the light of subsequent experiments. The plants grown in air slightly enriched with CO_2 had not only smaller leaves than the controls, but these leaves were of a distinctly darker green, and the internodes of the plants were decidedly shorter.

The results obtained with these preliminary experiments now induced us to extend our observations to a larger number of species, and arrangements were consequently made to carry out a series of experiments on a large scale, and under conditions which would admit of the plants being kept under observation for a much longer period of time.

For this purpose a small greenhouse adjoining the Jodrell Laboratory was kindly placed at our disposal by the Director. This was divided into two compartments, each of about 380 cubic feet capacity, by means of a glazed partition, which was made quite air-tight. In one of these, compartment A, the experimental plants were grown in normal air, whilst the air of compartment B could be enriched to any desired extent with carbon dioxide supplied from a receiver of the liquefied gas placed in an adjoining building. The gas before entering the greenhouse was bubbled through a wash-bottle at a rate which previous experiments had shown to be necessary in order to keep the composition of the air approximately constant. Frequent analyses of the air in both compartments were made as a check.

The current of carbon dioxide was started each day at 6 A.M., and continued until 6 P.M., both greenhouses being closed during the day, and the glass top and sides of the houses were white-washed over in order to exclude direct sunlight, whilst at the same time allowing plenty of illumination. During the night both greenhouses were opened and well ventilated from the outside, so that for 12 hours out of the 24 the atmospheric conditions were identical. Care was taken to maintain the temperature, degree of illumination, and the hygroscopic state of the two compartments as nearly as possible identical, the only point of difference being in the composition of the air.*

* The plants were grown in a rich garden soil containing all the mineral and nitrogenous constituents necessary for luxuriant growth.

Two series of experiments were made, one in the summer of 1900, and the other in the summer of 1901.

The composition of the air as regards carbon dioxide differed very much in these two experiments, in one case the air being enriched with about 5·5 to 6 *per cent.* of the gas, *i.e.*, 180 *to* 200 *times* the normal amount, whilst in the other case the mean CO_2 content was only 0·114 *per cent.*, i.e., *between three and four times* the normal amount.

Contrary to what might have been expected, the general results, compared with those obtained with the control plants in ordinary air, were practically identical in the two sets of experiments, notwithstanding the large range of something like 1 to 50 in the CO_2 content of the enriched air.

Since the greater interest attaches to the experiments with the smaller increment of CO_2, we shall confine our attention almost entirely to this set in the remarks which follow.

The plants taken for this experiment were as follows :—

(1.) 8 plants of *Cucurbita Pepo* (Italian Gourd).
(2.) 8 ,, ,, *Impatiens platypetala.*
(3.) 6 ,, ,, *Nicotiana affinis.*
(4.) 6 ,, ,, *Nicotiana sylvestris.*
(5.) 10 ,, ,, *Begonia gracilis.*
(6.) 6 ,, ,, *Solanum atropurpureum.*
(7.) 12 ,, ,, *Kalanchoë Welwitschii.*
(8.) 6 ,, ,, *Fuchsia*, var. with light coloured leaves.
(9.) 6 ,, ,, *Fuchsia*, var. with darker leaves.

One-half of each set was placed in compartment A, the other half in compartment B, the plants being carefully matched as regards size and general appearance, and arranged symmetrically as regards the glass division separating the two compartments,

Set A in ordinary air (controls).

Set B in air enriched with CO_2.

The experiment was commenced on May 13, and continued until July 29, *i.e.*, for a period of 77 days.

The mean content of the air in CO_2 *during the daytime* was :—

In compartment A, 3·29 parts per 10,000.
,, ,, B, 11·47 ,, ,, ,,

So that the atmosphere of compartment B contained during the daytime about three and a-half times more CO_2 than that of compartment A.

A careful record was made of the differences in appearance of the two sets of plants on June 10, June 29, and July 13, that is to say, at 28, 47, and 61 days from the commencement of the experiment. The results are given in detail in the Appendix to this paper, and may be summarised as follows :—

The effect of an increased amount of CO_2 in the air becomes in most cases apparent within a week or 10 days from the commencement of the experiment, and rapidly increases as times goes on. There is a marked difference induced in the habit and general appearance of most of the plants owing to a stimulation of all axial growth, accompanied by a more or less pronounced shortening and thickening of the internodes. Usually, but not in all cases, there is an increased number of the internodes, so that the height of the two contrasted sets remains much about the same, but the chief difference of general habit is brought about by the development throughout the plant of secondary axes in the axils of the leaves, thus giving the plants grown under the influence of increased CO_2 a denser and more bushy appearance. This was particularly noticeable in the *Fuchsias*, especially the dark-leaved variety, in which every axil bore a shoot, and frequently extra axillary ones. Adventitious shoots were also developed rather freely at the base of the plants.

The leaf area of the plants under the influence of increased CO_2 was generally found to be much reduced, not so much by the formation of a less number of leaves as by the reduction in area of the individual leaves. This was found to be extreme in the case of the dark-leaved *Fuchsias*, and it was also very marked in the second crop of the leaves of *Impatiens*. There was also produced in many of the plants a marked inward curling of the leaves, the extremes in this direction being found in the *Begonias* and *Fuchsias*. In the dark-leaved variety of *Fuchsia* the leaves were curled inwards like a watch-spring, which would doubtless tend to reduce excessive photosynthesis by preventing the normal amount of light from reaching the chloroplasts. This change of habit may in fact be regarded as an attempt on the part of the plant to adapt itself to its abnormal atmospheric surroundings.

The extra CO_2 in several cases induced a deeper green colour in the leaf, and in all other parts of the plant where chlorophyll was present. This was particularly noticeable in the second crop of leaves developed on the *Impatiens*, in the *Begonias*, and in the darker-leaved *Fuchsias*.

On July 19, the Sachs test for starch was applied to the leaves of the two varieties of *Fuchsia*, *Cucurbita Pepo*, and *Impatiens platypetala*. In all cases the leaves taken from the plants grown with increased CO_2 in the air showed a much larger accumulation of starch than did the leaves of the control plants. These differences were the most strongly marked in the leaves of *Impatiens*, which became quite black with the test.

It was, however, in the development of the *reproductive organs* of the two sets of plants that the most striking and important differences were found. Whilst the control plants in ordinary air flowered and in some cases fruited luxuriantly, in the corresponding plants sub-

mitted to air containing 11·4 parts per 10,000 of CO_2, *inflorescence was almost totally inhibited.* With the exception of one or two sickly looking flowers on the *Begonias*, not a single flower-bud opened on any of the plants of this set. The plants of *Impatiens*, *Kalanchoë*, and of the darker-leaved *Fuchsias*, did not even produce a flower-bud, whilst in the *Nicotiana*, *Cucurbitas*, and lighter-leaved *Fuchsias*, the small flower-buds which commenced to form were completely shed long before the time of opening.

The plants which appeared to be most sensitive to the action of the extra CO_2 in the earlier stages of growth were those of *Impatiens platypetala*, which from the commencement presented a strong contrast to the healthy appearance of the controls. They lost nearly all their leaves, and the bare stems shed many of their internodes, which were cut off successively just above the nodes. By June 29, however, the plants had begun to recover, and, by putting out a second growth of small and very dark green leaves, indicated a certain limited adaptation to their abnormal atmospheric environment.

So far only the more striking visible differences between the two sets of plants have been described. It is highly probable that these will be found correlated with equally well-marked differences of anatomical structure. This part of the enquiry has been kindly undertaken by Professor J. B. Farmer and Mr. S. E. Chandler, who will embody their results in a separate communication.

In another series of experiments, which we carried out on similar lines, the air of compartment B was enriched with carbon dioxide to the extent of 6 *per cent.*, that is to say, up to about 200 times the normal amount. The plants used in this experiment were as follows :—

Nicotiana sylvestris.	*Ricinus communis*, red variety.
,, *tomentosa.*	*Chrysanthemum Broussonettii.*
Solanum giganteum.	*Begonia multiflora.*
Fuchsia.	*Kalanchoë rosea.*
Ricinus communis, green variety.	*Cucurbita Pepo.*

The experiment extended from June 3 to August 26, and the general results both in the direction and amount of change of habit induced in the plants were so very similar to those induced in the plants with only three and a-half times the normal amount of CO_2, as to require no further special description. The results are, however, valuable as indicating that the observed differences cannot be due to any *direct* poisonous influence of the carbon dioxide, otherwise we should certainly expect a marked difference to be produced by increasing the amount of CO_2 from 11·4 parts per 10,000 to 600 parts per 10,000, *i.e.*, more than fiftyfold, which was not the case to any appreciable extent.

The direction in which we must search for the true explanation of

the effect is probably indicated by the experiments on leaves described in the early part of the paper, where it was shown that the amount of photosynthesis in the leaf lamina is, within certain ill-defined limits, a function of the partial pressure of the CO_2 in the surrounding air.

In the first series of experiments in the greenhouse, where this partial pressure was maintained at about three and a-half times the normal, the plants for a certain limited period must have been manufacturing carbohydrate material within their chloroplasts at least three and a-half times faster than those in normal air, and, although this rate of photosynthesis would perhaps not be maintained for very long, yet there would always be a general tendency for the carbohydrate supply in the leaves to be kept up to a higher point than in the controls grown in ordinary air, a fact which was shown by the leaves of set B always being gorged with starch.

Since it is quite certain that this increased photosynthesis does not to any material extent contribute to the increase of dry weight of the plants, we can only conclude that the transformation, translocation, and general metabolism of the leaf-reserves under these conditions cannot keep pace with the increased tendency to produce an extra amount of plastic material from the atmosphere. Moreover, it is clear that the whole mechanism of the plant on which normal nutrition depends has its parts so completely and accurately correlated that any slight increase in the composition of the surrounding air which favours increased photosynthesis destroys the adjustment of the various parts and results in a more or less abnormal development of the plant. That any such disturbance of the economy of the plant should profoundly modify the reproductive functions, might perhaps have been expected.

It is somewhat remarkable to find that all the species of flowering plants, without exception, which have been the subject of experiment, appear to be accurately "tuned" to an atmospheric environment of 3 parts of CO_2 per 10,000, and that the response which they make to slight increases in this amount, are in a direction altogether unfavourable to their growth and reproduction. It is not too much to say that a comparatively sudden increase of carbon dioxide in the air to an extent of but two or three times the present amount, would result in the speedy destruction of nearly all our flowering plants.

To a certain extent we may regard the facts recorded in this paper as indicating that the composition of our atmosphere as regards its carbon dioxide, has remained constant, or practically constant, for a long period of time, but they leave altogether untouched the question of any variations of a secular kind. All we are justified in concluding is that if such atmospheric variations have occurred since the advent of flowering plants, they must have taken place so slowly as never to outrun the possible adaptation of the plants to their changing conditions.

Appendix.

Details of the experiments made on Plants in Greenhouse. One set A grown in ordinary air, the other set B grown in air containing 11·47 *parts of* CO_2 *per* 10,000.

For list of these plants, see p. 407.

The experiment was commenced on May 13.

(1.) *Cucurbita Pepo.*

June 10.—The only difference observable between the two sets of plants, was that a much less number of flower-buds was developing on the plants of set B in air with extra CO_2.

June 29.—The development of the flower-buds on the plants grown in extra CO_2 was now completely arrested.

July 13.—A well marked difference between the two sets. Those of set A, in ordinary air, had formed flower-buds in all the axils and were flowering luxuriantly. The plants of set B (extra CO_2) were much the taller, owing to an increased number of internodes. There was also a considerable tendency to the production of secondary axillary shoots instead of flower-buds, whilst all the flower-buds which had formed had long since fallen off before they were fully developed.

(2.) *Impatiens platypetala.*

June 10.—All the four plants of set B (extra CO_2) were very unhealthy in appearance, having lost nearly all their leaves, and with no vestige of a flower-bud. The controls of set A in ordinary air were very healthy in appearance, and were bearing numerous flowers. (See Plate 5.)

June 29.—The plants of set B (extra CO_2), after losing their leaves, proceeded to shed certain internodal parts of their axes just above a node, and this process was in some cases repeated for some distance down the axis. On this date the plants were showing signs of recovery, and had produced a second crop of small and very dark green leaves.

The control plants A, in ordinary air, were normal in every way, and had just finished flowering.

July 13.—There was still a very marked difference between the two sets. Those of set A (ordinary air) were somewhat the taller, the axes being more divergent and the leaves not so closely set. The leaves were also larger and lighter green than those of B. Set B (extra CO_2). The plants had now recovered, and acquired a fairly healthy appearance. There were no flower-buds formed, and the leaves (second crop) were much smaller and darker in colour than those of set A.

(3.) *Nicotiana affinis.*

June 10.—Each set of plants had thrown up a flowering axis which in set B (extra CO_2) was not quite so fully developed, but whereas the flower-buds of the control plants in ordinary air had, in several cases, opened normally, the buds of set B (extra CO_2) were much fewer in number, very small, and showed no signs of opening. (See Plate 6.)

June 29.—The difference was now very striking. The plants in ordinary air had flowered well, but the set B, subjected to extra CO_2, although possessing well-developed flowering axes, had borne no flowers at all, the buds having been arrested in development.

July 13.—There were the same well-marked differences between the sets as when last noted. The plants in extra CO_2 had now thrown up several secondary axes from their base.

(4.) *Nicotiana sylvestris.*

June 10.—Set A, grown in ordinary air, were further developed than those of B, and possessed larger leaves.

June 29.—The same difference as on June 10. No flowers formed on plants in extra CO_2, whereas the controls flowered freely.

July 13.—The same remarks apply as on June 29.

(5.) *Begonia gracilis.*

June 10.—The six plants of set A, grown in ordinary air, were healthy and had flowered well. Those of set B (extra CO_2) appeared very unhealthy, and in only one instance showed any flowers, which were small, greenish, and altogether abnormal. (See Plate 7.)

June 29.—Whilst the control plants grown in ordinary air were in full flower, those of set B grown in extra CO_2 had only a few small, unopened buds, which dropped off before they opened.

The general appearance of the plants grown in extra CO_2 had now become fairly healthy, but there was an abnormal tendency for their leaves to curl downwards and inwards.

July 13.—A very marked difference in the two sets. Whilst the height was about the same the axial organs of set B, grown in extra CO_2, were much stouter than those of the controls, whilst the internodes were shorter and more numerous. The plants grown in ordinary air had a more spreading and less dense habit, whilst the leaves of set B (extra CO_2) had still a marked tendency to curve downwards and inwards, their colour being on the whole a darker green.

Whilst the plants in ordinary air had flowered and fruited well, those grown in extra CO_2 had either cast their buds entirely, or in some few cases these had developed into small, sickly, abnormal flowers, which in no case fruited.

(6.) *Solanum atropurpureum.*

June 10.—The leaves of set B (extra CO_2) were somewhat curved downwards, and the axes were distinctly higher than those of the controls. The spines on the leaves and stems were not so fully developed as on the control plants in ordinary air. (See Plate 8.)

June 29.—It was very remarkable to note how the axis of each plant of set B (extra CO_2) had become elongated as compared with the controls. There was also a less marked development of spines in the former case.

July 13.—There was now a very marked difference between the habits of the two sets. Without exception the plants of set B (grown in extra CO_2) were much taller. The height of the three plants in extra CO_2 was found to be from 23 to 24 inches, and the number of internodes 23 to 24, the average length of the internodes, therefore, being about 1 inch. In set A, grown in normal air, the height was about 14 inches, and the number of internodes about 16; so that the average length of the internodes in this latter case was about 0·8 inch. There were more internodes on the plants grown in extra CO_2, and they were somewhat longer.

There were about twice as many leaves on the plants grown in ordinary air, and the spinous hairs were more closely crowded together on these control plants, were stronger in growth, and of a deeper purple colour. No flowers had been developed on the plants of set B, grown in extra CO_2.

(7.) *Kalanchoë Welwitschii.*

June 10.—The control plants of set A in ordinary air were the better grown, and possessed larger leaves than those of set B (extra CO_2).

June 29.—There was but little difference in the height of the two sets, but the contrast as regards the size of the leaves was still very marked.

July 13.—The differences in the direction already indicated were still more pronounced.

(8.) *Fuchsia.*—(a) *Variety with Lighter Leaves.*

June 10.—The plants of series B, grown with extra CO_2, were not quite so tall as the controls, and their leaves were smaller. The flower-buds of this set commenced to develop, but soon dropped off after becoming very green.

June 29.—The habit of the plants grown in extra CO_2 was a little denser than that of the controls. Whilst the controls (in ordinary air) were flowering copiously, the flower-buds of set B (in extra CO_2) became green and were shed before they opened.

July 13.—In no single case had a bud opened on the plants grown in air containing increased amounts of CO_2, and their denser habit was still more strongly marked. The leaves were also smaller, of darker green and with a tendency to curl up, whilst the internodes were a little stouter, and shorter, and the colour of the axes was a little more pink.

(9.) *Fuchsia.*—(b) *Darker-leaved Variety.*

June 10.—There was already a marked difference between the two sets as regards general habit and appearance. The control plants in normal air possessed long and slender axes and were freely developing flower-buds. Set B, grown with extra CO_2, had a very abnormal appearance; their main axes were much shorter, whilst the leaves were extremely small and curled inwards; there was also a great development of axillary shoots, and adventitious ones at the base of the stems. (See Plate 9.)

June 29.—The above difference had become still more accentuated. No flowers had been formed on set B, grown with extra CO_2 in the air.

July 13.—The differences between the two sets were now extreme. The plants of set B (extra CO_2) had a most abnormal appearance. Their leaves were all extremely small, of a much darker green, and were rolled up in an inward spiral like that of a watch-spring. There was also a profuse development of secondary axes in the axils of most of the leaves, from the base of the primary axis up to its apex. This habit of growth gave the whole plant a much denser appearance than that of the control plants grown in ordinary air. The internodes were on the whole shorter and stouter than those of the controls, and differed markedly in colour: whereas those of the controls had the ordinary blood-red appearance, the internodes of the plants grown in extra CO_2 were pinkish-green. No flowers had developed on the plants of set B, grown in extra CO_2. (See Plate 10.)

DESCRIPTION OF THE PLATES.

Plate 5.—*Impatiens platypetala.*

Under experiment for 28 days.

A. Plants grown in ordinary air.

B. „ in air containing 11·4 parts per 10,000 of CO_2.

Plate 6.—*Nicotiana affinis.*

Under experiment for 28 days.

A. Plants grown in ordinary air.

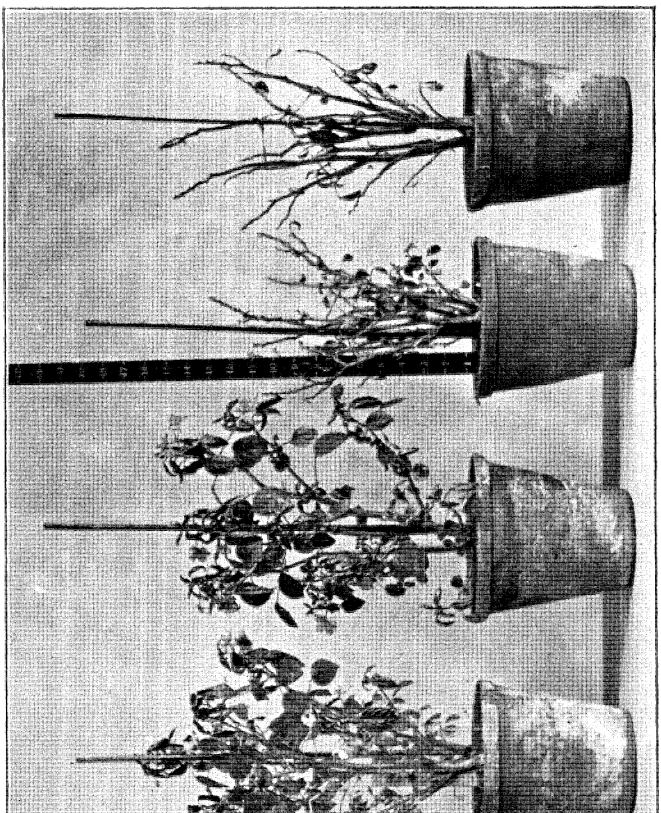
B. „ in air containing 11·4 parts of CO_2 per 10,000.

Plate 7.—*Begonia gracilis.*

Under experiment for 28 days.

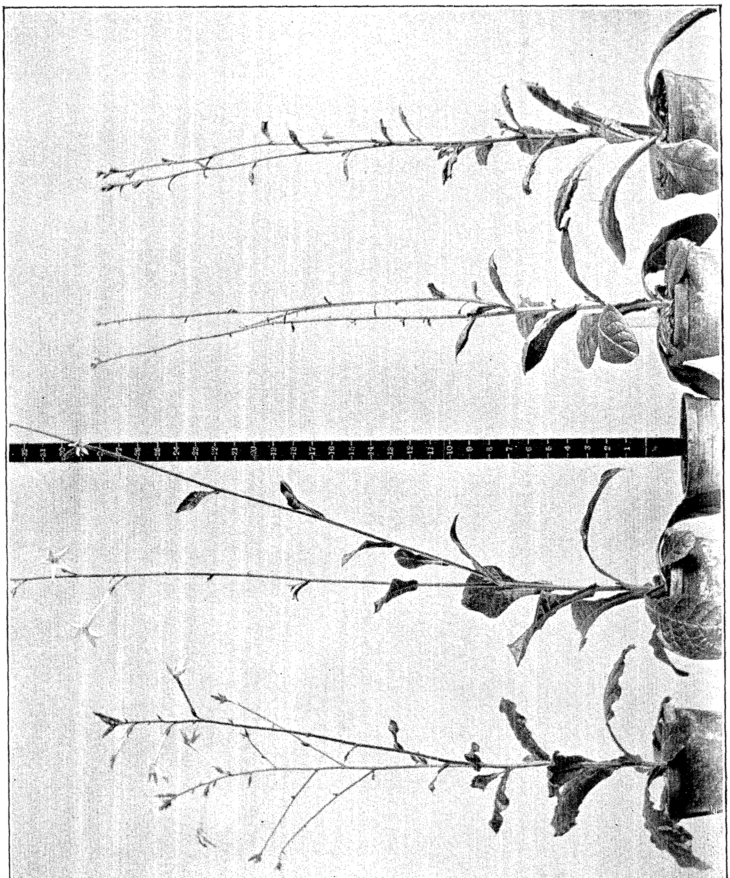
A. Plants grown in ordinary air.

B. „ in air containing 11·4 parts of CO_2 per 10,000.



A B

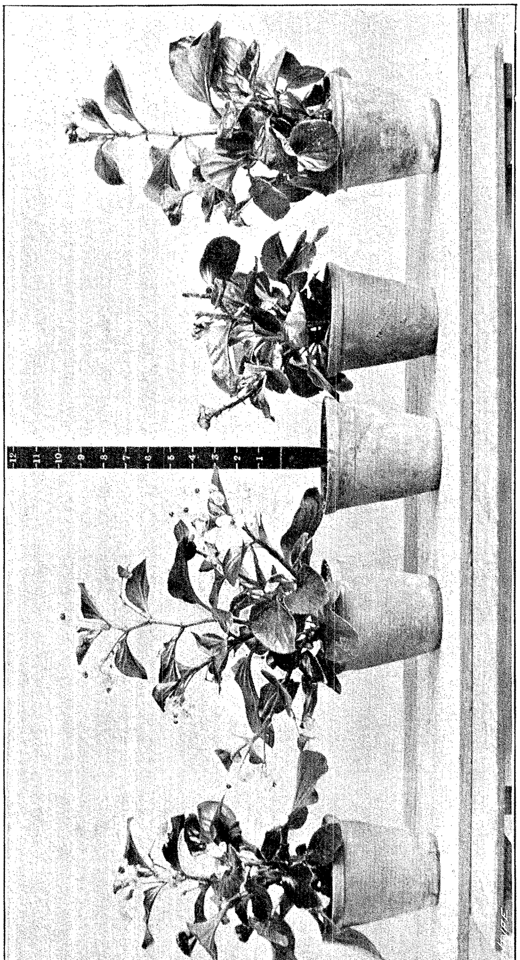
PLATE 5.



A

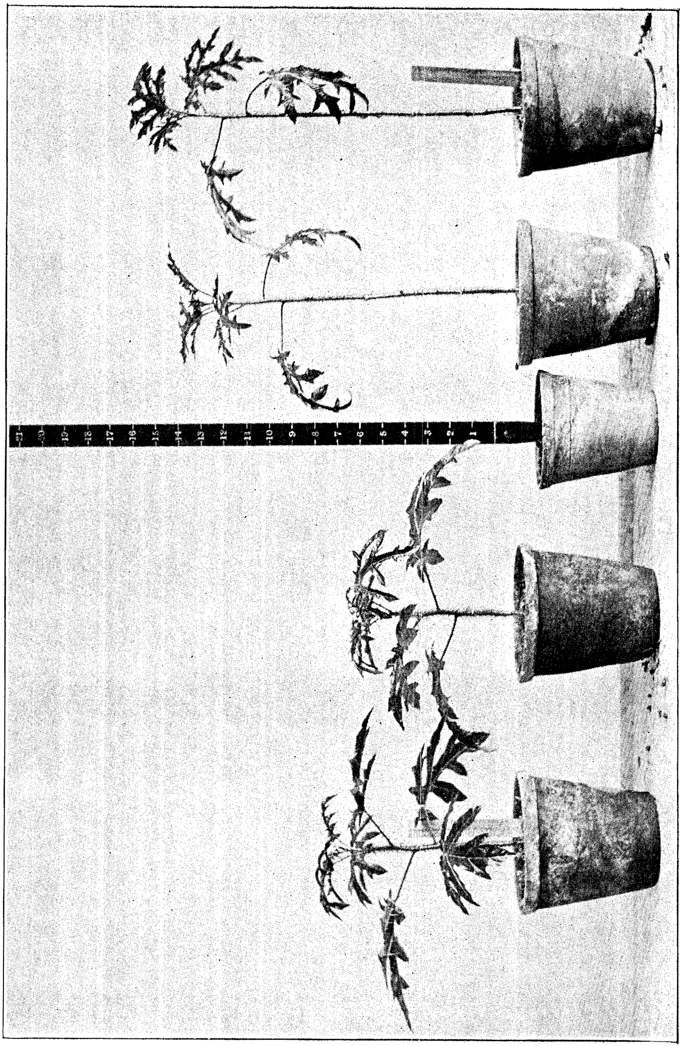
B

PLATE 6.



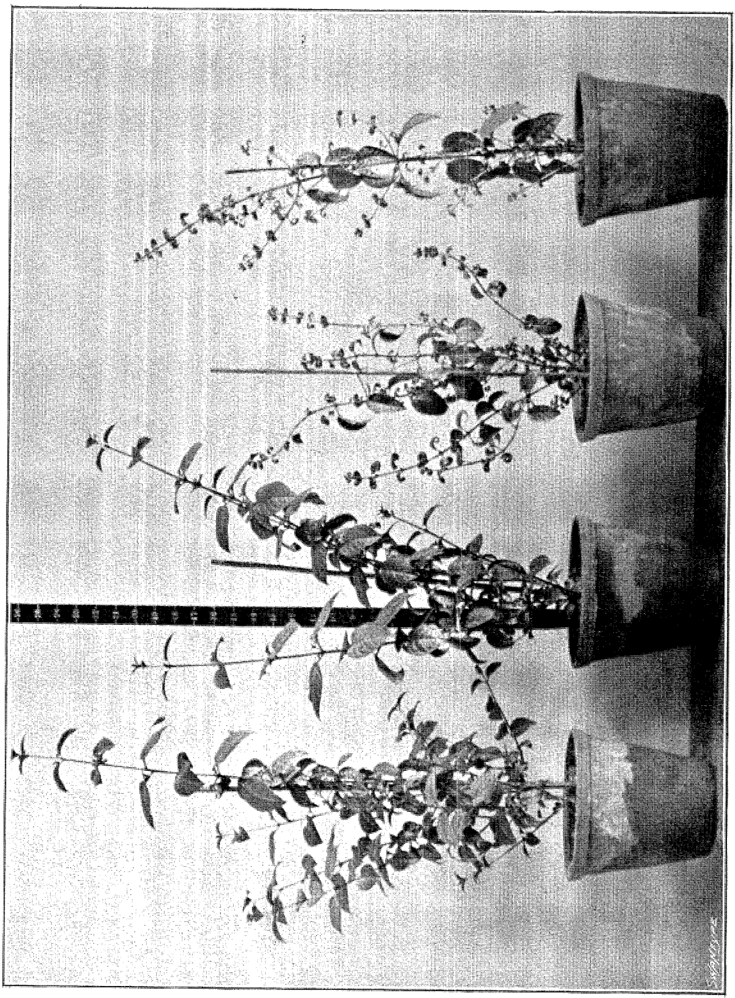
A B

PLATE 7.



A B

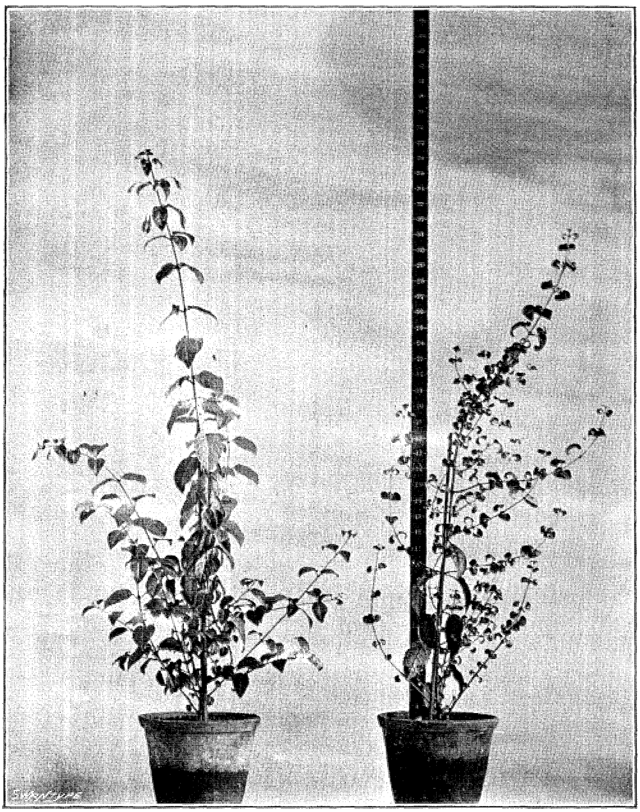
PLATE 8.



A

B

PLATE 9.



A B

PLATE 10.

Plate 8.—*Solanum atropurpureum.*

Under experiment for 28 days.

A. Plants grown in ordinary air.

B. „ in air containing 11·4 parts of CO_2 per 10,000.

Plate 9.—*Fuchsia.* Dark-leaved variety.

Under experiment for 28 days.

A. Plants grown in ordinary air.

B. „ in air containing 11·4 parts of CO_2 per 10,000.

Plate 10.—*Fuchsia.* Dark-leaved variety.

Under experiment for 54 days.

A. A plant grown in ordinary air.

B. „ in air containing 11·4 parts of CO_2 per 10,000.

N.B.—The scale on the rod is in inches.

"On the Influence of an Excess of Carbon Dioxide in the Air on the Form and Internal Structure of Plants." By J. BRETLAND FARMER, D.Sc., F.R.S., Professor of Botany in the Royal College of Science, London, and S. E. CHANDLER, A.R.C.S. Received May 6,—Read May 29, 1902.

The plants which form the subject of the present enquiry were kindly handed over to us by Messrs. Horace Brown and F. Escombe. They were preserved in alcohol, and had previously served as the material on which the researches of these investigators on the influence of varying amounts of carbon dioxide in the air on the photosynthetic processes of leaves and on the mode of growth of plants* had been conducted.

The series, consisting of the following five plants, viz., *Kalanchoë Welwitschii*, *Solanum atropurpureum*, *Begonia gracilis*, *Impatiens platypetala*, *Fuchsia*, sp., included in every case specimens which had been grown in a greenhouse in ordinary air containing 3·29 parts of carbon dioxide in 10,000 volumes of air, and others that had been cultivated under conditions as similar as possible except that the atmosphere contained about 3·5 times (11·47 per 10,000) the amount of carbon dioxide normally present in ordinary air. For the sake of brevity we shall refer to them as the *air* or control and as the *CO_2* plants respectively.

We directed our attention more especially to the following points:—

(1.) The relative dimensions of the internodes.

* *Cf.* H. Brown and F. Escombe, "On the Influence of Varying Amounts of Carbon Dioxide in the Air on the Photosynthetic Processes of Leaves and on the Mode of Growth of Plants," 'Roy. Soc. Proc.,' vol. 70, in which full details are given as to the methods of experiment and the external appearances presented by the plants.

A B

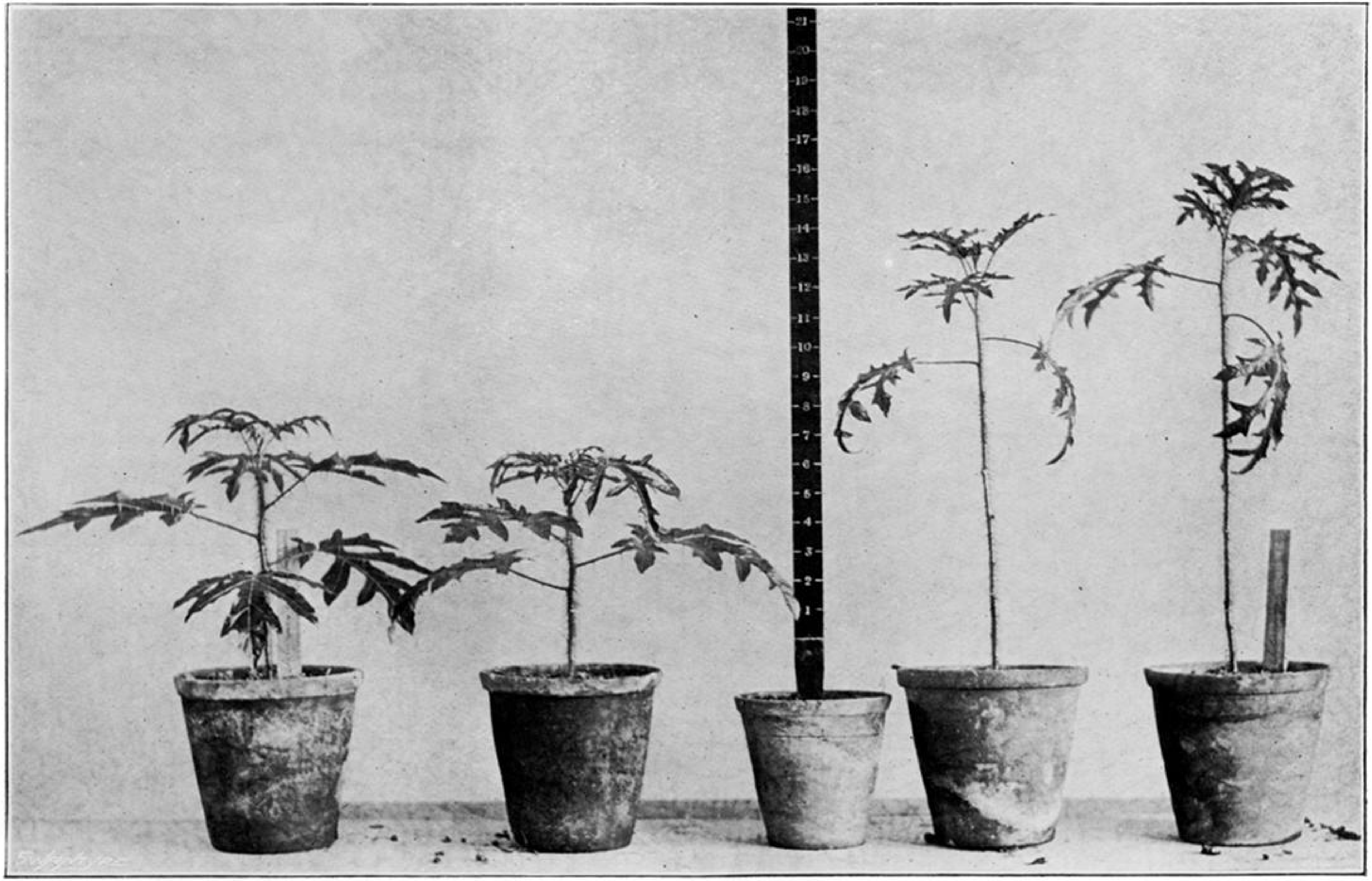
PLATE 5.

A B

PLATE 6.

A B

PLATE 7.

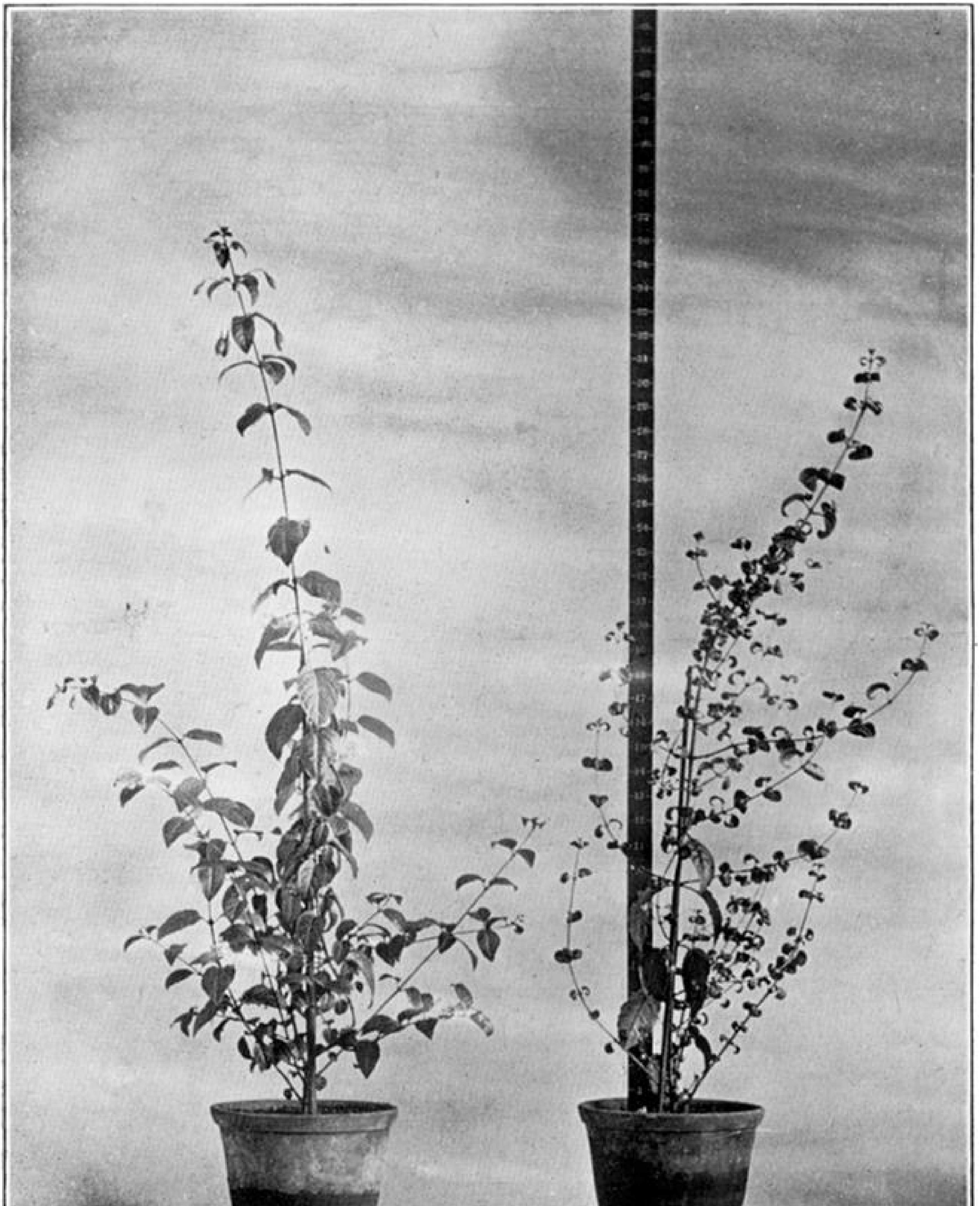


A B

PLATE 8.

A B

PLATE 9.



A B

PLATE 10.